

Modelling and Monitoring Ecosystem Responses to Climate Change in Three North American Mountain Ranges

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INTRODUCTION

Mountains play a significant role in human activities, providing critical resources such as minerals, forest products, and 50% of the freshwater consumed by people (Liniger *et al.*, 1998). Recently, mountains assumed a different strategic role because they are now recognised as important reserves of biodiversity, with potential value that we are just beginning to comprehend (Messerli and Ives, 1997).

Mountain protected areas and biodiversity

Mountains have greater biodiversity than their lowland counterparts because steep environmental gradients compress life zones, resulting in large species turnover over short distances (Beniston and Fox, 1996). Rugged mountain topography leads to higher rates of endemism through genetic isolation, and many mountain areas have been refugia for species during past climate changes. Lastly, mountains historically have been less altered by humans because of the harsher climate and logistical difficulties inherent in mountain living. Thus, the loss of biodiversity in agricultural and urban areas has not been mirrored to the same extent in the mountains. Mountain environments are better represented than lowlands in the world's inventory of parks and protected areas and, in the United States, many national parks were established *before* increasing human populations significantly modified the region. Although mountain ecosystems have retained their inherently greater biodiversity more than

human-dominated environments, new pressures have led to mountain ecosystems being declared one of the Earth's most threatened resources. Stress caused by climate change may be more profound and occur earlier in mountains because of their steep climatic gradients (Oerlemans, 1994). Climate change will interact more with direct human activities, such as deforestation and habitat fragmentation, to severely threaten extant biodiversity of mountain ecosystems.

Climate change research at US mountain National Parks

We describe in this paper a multi-scale, multi-disciplinary approach examining how climatic change and variability drive ecosystem dynamics in three North American mountain protected areas – Olympic, North Cascades, and Glacier National Parks (Figure 20.1). Olympic and Glacier National Parks have been part of the US National Park Service (NPS) and US Geological Survey Global Change Research Program (GCRP), established by Congress in 1990 to look at impacts of global change on park natural resources. National Parks are excellent sites for climate change detection and research because it is easier to attribute changes in relatively pristine natural systems to regional and global-scale climatic shifts rather than local, human factors. National Parks represent an increasingly unique condition in which the original species and relationships are largely unaltered and available for study. Lastly, park management needs to know how

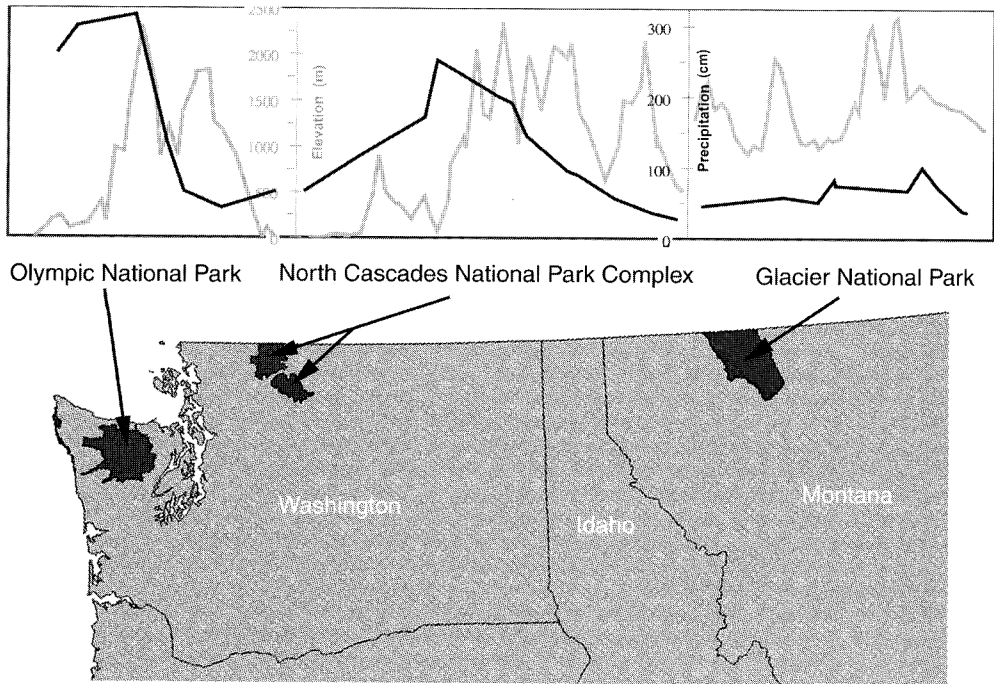


Figure 20.1 National parks dominated by mountains along the United States and Canadian border (49°N). A transect from Olympic National Park to Glacier National Park represents gradients in climatic variability and surrounding land use

climate change will affect the biodiversity they are charged with protecting. Because park boundaries are fixed and species responses to environmental gradients are spatially dynamic, under future climatic conditions many parks may contain different flora and fauna.

Although these protected areas are relatively pristine, they already have been subjected to climate change. For example, at Glacier National Park, glaciers have been reduced to mere remnants of their previous sizes and over two-thirds of the estimated 150 glaciers have disappeared since 1850 (Carrara, 1989), leaving approximately 37 today (Key *et al.*, 1997). Because glacial meltwater can be critical for stream baseflow in late summer, there are significant ecological implications of glacier disappearance in park watersheds. Temperature-sensitive stream organisms such as net-spinning caddisflies (e.g. *Hydropsyche* spp.) may become less abundant, shift distribution or disappear as summer water temperatures increase in the

future, without glacial meltwater to keep streams flowing with cold water (Fagre *et al.*, 1997). Major changes in glacial extent strongly indicate other fundamental changes in mountain ecosystems are occurring at Glacier and Olympic National Parks. Since 1990, different approaches were taken at each park to identify climatically-driven shifts in species distribution, species growth patterns, and ecosystem processes. As studies incorporated broader scales and regional landscape connections, the separate research groups coalesced. We summarise here the achievements of this diverse group, whose individual contributions are cited throughout this paper and who are listed in the Acknowledgements.

STUDY AREAS

Glacier, North Cascades and Olympic National Parks are large, wilderness-dominated parks near the United States–Canada border in the

northern Rocky Mountains, the Cascade Mountains and on the Olympic Peninsula, respectively (Figure 20.1). Each park encompasses mountains with similar topographic relief, numerous glaciers and expansive conifer forests; each is snow-dominated, acts as the headwaters for its region and contains relatively intact floral and faunal assemblages. Climate is controlled by dominant air masses, providing Olympic with a maritime climate, North Cascades a transitional climate, and Glacier with a more continental climate. Thus, winter temperatures are moderate in the Olympics and cold in the northern Rockies. Summer precipitation as a proportion of annual precipitation is greater in the northern Rockies than in Olympics. Precipitation varies dramatically between westside and eastside locations within each park. For example, precipitation in the Olympic Mountains ranges from $> 600 \text{ cm yr}^{-1}$ on Mt Olympus to only 40 cm yr^{-1} in the northeastern rainshadow. Precipitation in the northern Rockies varies from 350 cm yr^{-1} (westside, high elevation) to 40 cm yr^{-1} (eastside, low elevation). This contrast in precipitation over relatively small distances has a profound impact on microclimate, vegetation distribution and disturbance regimes. Vegetation is dominated by coniferous forest, with species distribution and abundance varying along elevational gradients (extending to alpine vegetation) and from westside to eastside (including grassland). The western Olympics are dominated at low elevations by temperate rain forests with high biomass and abundant woody debris. Biomass and productivity generally are lower in the northern Rockies. The parks have 10 coniferous species and several plant communities in common, which allows comparisons of biotic responses to climatic shifts.

Lake McDonald and St Mary watersheds in Glacier National Park

The modelling approaches were developed initially in the Lake McDonald watershed and later applied to St Mary watershed (Figure 20.2). Lake McDonald watershed is a 462-km^2 forested watershed on the western slopes of the



Figure 20.2 Map of Glacier National Park with McDonald and St Mary drainages. Much of the model development and validation took place in McDonald drainage area

continental divide in the park. Elevation ranges from 948 m at the outlet to 2895 m in the alpine areas of the watershed. Approximately 75% of the watershed is forested, predominantly by conifers. Seven second-order streams drain the basin and flow into Lake McDonald. The watershed encompasses more than a dozen small lakes and approximately 250 km of streams and rivers. The basin comprises a mix of argillaceous limestones and tertiary sediments deposited by repeated glaciations. The St Mary watershed and St Mary Lake are similar in most respects to Lake McDonald, except that there is a distinct shift to more arid-adapted species, less biomass, more open forest canopies, reduced extent of forests and more expanses of grass.

RESULTS

Ecosystem modelling and monitoring in large landscapes

To address how climate change would alter western mountain National Parks, we chose a combined approach of ecosystem modelling and long-term monitoring. Few natural

Regional Hydro-Ecological Simulation System (RHESSys)

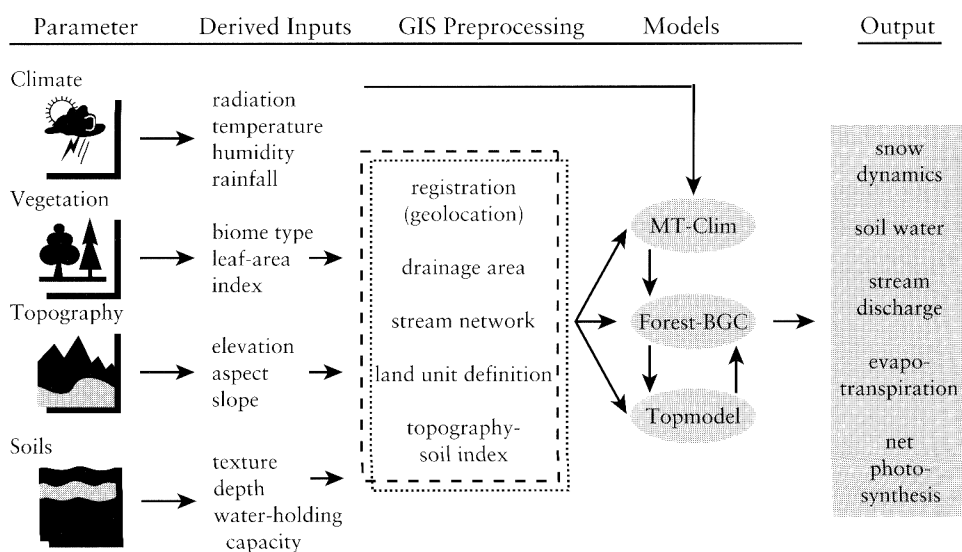


Figure 20.3 Schematic of RHESSys organization depicting data inputs and ecosystem outputs. See text for details

resources have been monitored in any National Park for more than two decades, so long-term studies were initiated in the Olympic, North Cascades, and Glacier National Parks to document changes with the knowledge that their value might be many years in the future. These monitoring efforts, however, also provided parameterisation and validation data for ecosystem models. To predict potential climate change effects, we initially established an ecosystem modelling framework for Glacier National Park under current climatic conditions. Ecosystem modelling is a necessary tool for organising complex relationships in the biophysical environment into a structured logic that can produce quantitative predictions with which field data can be integrated and compared. Ecosystem models, once tested and validated, can help us to understand responses to climate change that at first seem counter-intuitive. An example is found in Running and Nemani's (1991) simulation of the response of a northwestern Montana forested watershed to a doubling of atmospheric CO_2 . Despite a 10% increase in annual precipitation, streamflow decreased by 30%, especially in late summer

because snowpack duration was diminished by 2 months and, with a longer growing season increasing annual photosynthetic production up to 30%, greater evapotranspiration losses from the watershed occurred. These results, if true, would profoundly affect the watershed ecosystems of the Glacier National Park area.

Ecological models

We further developed the Regional Hydro-Ecological Simulation System (RHESSys) and FIREBGC (Fire-BioGeoChemical) models and applied them to Glacier National Park to answer questions about the state of natural resources and biodiversity in the future using several climate change scenarios.

RHESSys is a collection of evolving tools and interacting models that can be customised for specific needs (Band *et al.*, 1993) (Figure 20.3). RHESSys utilises remotely-sensed data from satellite platforms, such as Landsat Thematic Mapper data, to calculate metrics such as the Normalised Vegetation Difference Index (NDVI) and Leaf Area Index (LAI) for specific landscapes (Running and Gower, 1991). NDVI

and LAI are coarse indices of vegetation function and structure that are applied to, or 'draped', over a Digital Elevation Model of Glacier Park within a Geographic Information System (GIS) to provide a three dimensional view of a cyber-ecosystem. A mountain climate simulator (MTCLIM) uses existing base station daily climate data to calculate daily variables (e.g. maximum and minimum temperatures, solar radiation, daily precipitation) for all slope, aspect, and elevation combinations (Thornton *et al.*, 1997). These daily simulated climate data, coupled with a soils map, are used by a core model component, FOREST-BGC, to estimate ecosystem processes, such as gross photosynthesis, and calculate ecosystem outputs, such as net primary productivity and hydrologic discharge. FOREST-BGC is a forest growth model that calculates tree responses to nutrients, moisture and energy, and incorporates algorithms that describe details like carbon allocation to roots and stems (Running and Gower, 1991). Responses to daily climate variables are summed over the year to estimate annual amount of carbon fixed, available nitrogen and other ecosystem attributes. RHESys is a flexible and modular system. Early in the project, a hydrologic routing model (TOPMODEL) was incorporated to account for subsurface water flow through topographically complex terrain and to estimate the daily flux in basin outflow (Band *et al.*, 1993). This proved to be effective, estimating both daily and annual stream discharge accurately when compared to actual stream discharge measurements (Fagre *et al.*, 1997). Recently improved routing models can easily be incorporated, underscoring the point that RHESys is continually evolving. The key products from RHESys for managers are spatially-explicit estimates of ecosystem responses to daily climate, displayed in a three-dimensional format.

FIREBGC is a companion model that is driven from the same forest process model, FOREST-BGC, as RHESys but has a focus on tree stand dynamics and responses to fire as a disturbance process (Keane *et al.*, 1996). FIREBGC is an individual tree model created by merging the gap-phase process-based model

FIRESUM with the mechanistic ecosystem biogeochemical model FOREST-BGC. It has mixed spatial and temporal resolution such that ecological processes that act at a landscape level, such as fire and seed dispersal, are simulated annually from stand and topographic information. Stand-level processes, such as tree establishment, growth and mortality; organic matter accumulation and decomposition, and undergrowth plant dynamics are simulated daily and annually. Tree growth is mechanistically modelled based on daily carbon fixed by forest canopy photosynthesis at the stand level. Carbon allocated to the tree stem at the end of the year generates the corresponding diameter and height growth. Outputs from FIREBGC include spatially-explicit estimates of tree species dominance, stem density, and forest floor biomass. These forest attributes help to determine the fuel loading and continuity necessary to generate stand-replacing forest fires. FIREBGC explicitly simulates long-term changes in fuels, fire hazard, fire behaviour and consequent effects on ecosystem characteristics of standing crop biomass, nitrogen cycling and leaf area index. FARSITE (Fire Area Simulator) is a model integrated with FIREBGC that maps fire extent and intensity for different climate conditions and successional trajectories in forest response. Thus, as the Glacier National Park cyber-ecosystem runs through daily cycles of climate and ecosystem response, these models allow us to 'see' — over a three-dimensional landscape — the changing structure and distribution of the forest, as well as the invisible ecosystem processes that underlie them.

How well do the models work?

Since 1992 we tracked daily, monthly, and annual dynamics of the Lake McDonald watershed and, less intensively, of the St Mary watershed. A key test was conducted by comparing daily estimates of temperature and precipitation with observed data from seven automated climate stations situated at various points in the watershed. These stations were placed to maximise topographic variability to

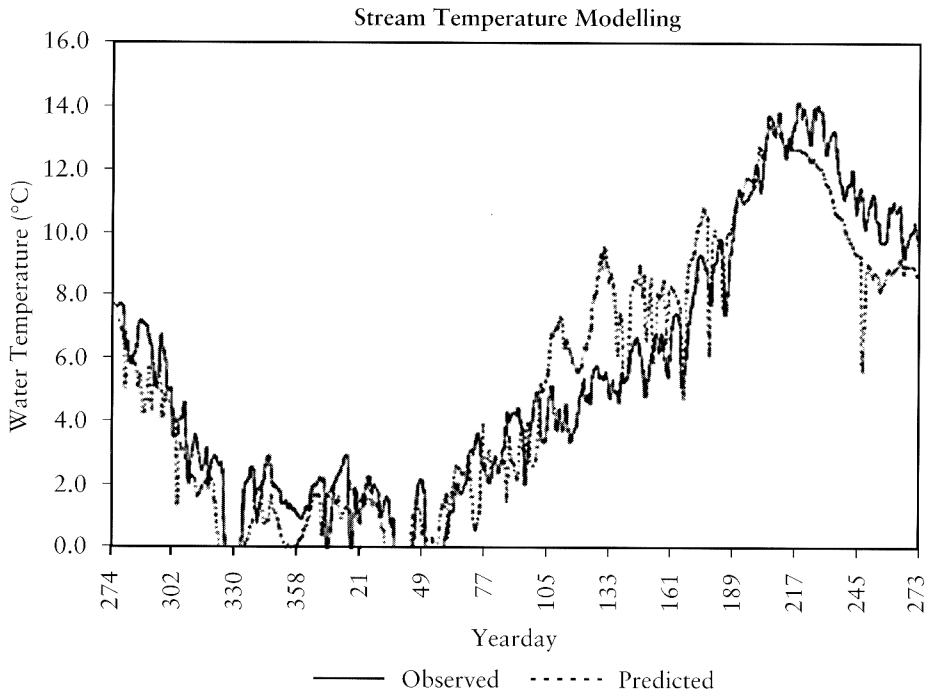


Figure 20.4 Relationship between predicted (simulated) and observed (measured) stream temperatures for McDonald drainage, Glacier National Park

test the full range of conditions within the watershed, i.e. different combinations of slope, aspect, and elevation. Snowpack characteristics, such as the snow water content, were generated by RHESSys from these climate station data and over 5 000 snow measurements were taken throughout the watershed for validation. Individual site snow measurements were well-correlated ($R^2 = 0.78$) with model estimates, but it was concluded that better estimates of snow sublimation in tree canopies depended upon accurate leaf area index (LAI) estimates (Fagre *et al.*, 1997). Because LAI was derived from Landsat TM data at 30 m pixel resolution, further improvements in satellite-based remote sensing will be necessary to improve snow estimates. However, at the watershed scale, the spatially aggregated snow water estimates were better correlated with observed values ($R^2 = 0.95$) (White *et al.*, 1998) and proved to be sufficiently accurate to provide close agreement between observed and simulated stream discharges

during spring run-off (Fagre *et al.*, 1997). Additionally, modelled estimates of stream temperatures throughout the watershed closely matched the annual temperature pattern from seven monitored streams (Figure 20.4) (Fagre *et al.*, 1997).

White *et al.* (1998) concluded that reasonable estimates of ecosystem processes were generated for Lake McDonald watershed by RHESSys. These included net primary productivity, evapotranspiration, available nitrogen and other outputs that characterise the major forest processes driving ecosystem change. Estimates of forest stand characteristics from FIREBGC were assessed with 100 circular plots (0.05-ha) located in stands typical of each plant community and distributed throughout the watershed by slope, aspect and elevation (Keane *et al.*, 1996). Tree structure, age, forest floor biomass, soil depth and texture and undergrowth canopy cover were measured on each plot. FIREBGC estimates provided reasonable agreement with field data. For

instance, trends in tree ring widths for the past 40 years generally agreed with FIREBGC predictions ($R^2 = 0.89$) (Keane *et al.*, 1996).

What do we do with the models?

With functional ecosystem models in hand, we addressed potential ecosystem responses to future environmental conditions rather than to current conditions. We chose an initial climate scenario that increased annual precipitation by 10% and annual temperature by 4 °C and found that the LAI increased about 40% as trees responded to better growing conditions. Ferguson (1997) evaluated four general circulation models and several downscaling approaches to provide a 'most likely' climate change scenario for the Columbia River Basin (of which Lake McDonald watershed is a part). This scenario projects a 30% annual precipitation increase and a 0.5 °C annual mean temperature increase by 2050. Applying these changes to Glacier National Park, we found a distinct shift toward more mesic tree species at lower elevations near Lake McDonald. Western red cedar (*Thuja plicata*) and hemlock (*Tsuga heterophylla*) expand in valley bottoms by 2050. This shift in tree species composition has significance for park management because these cedar–hemlock groves are currently the easternmost distribution of these tree species and receive special consideration during decision making. The cedar–hemlock plant association includes devil's club (*Oplopanax horridum*) and a variety of other species more typical of the humid Pacific northwest forests that contribute to the biodiversity of the park. Other dominance shifts include a reduction in subalpine fir (*Abies lasiocarpa*) as treelines rise and a significant expansion of Engelmann spruce (*Picea engelmannii*) at the expense of lodgepole pine (*Pinus contorta* var. *latifolia*). Although these are only estimates of future conditions, the results underscore the potential for changes in the species composition at Glacier National Park.

We also examined the effects on Glacier National Park ecosystems of an extremely variable climate but without long-term increases in

temperature or precipitation. Overall conifer net primary productivity decreased between 4% on the western side of the continental divide and 13% on the eastern side (White *et al.*, 1998) but broad-leaved shrubs and alpine vegetation increased 2–7%. However, the interannual variation in productivity for all vegetation types except conifers increased as much as 110%. Adding disturbance factors such as fire, a 120-year simulation indicated net primary productivity decreases for the eastern side of the park in the St Mary watershed but the western side of the park became more productive by 3000 kg of carbon per hectare annually. These potential changes would cause significant shifts in vegetation composition because the lowered productivity of the St Mary watershed changes the long-term dynamic to favour grasses. In fact, the lower treeline (the forest–grassland ecotone) rises under the variable scenario, permanently reducing the amount of forest cover in the St Mary watershed.

The models can spatially identify areas of greatest potential biodiversity change, essentially mapping vulnerable parts of mountain ecosystems. We compared the difference between current and future water temperatures in Lake McDonald watershed under a climate change scenario (Figure 20.5). The areas with greatest temperature change, rising + 4.5 °C, would seem to be the most sensitive to climate change and likely have significant shifts in alpine stream insect populations. This would also be a logical place to focus monitoring efforts, alerting managers to more pervasive changes going on throughout the park.

Wildland fire is the primary disturbance process in northern Rocky Mountain forests and greatly influences carbon cycles in mountain ecosystems. Fire infrequently burns upper elevation forests but fire suppression is one cause for the decline of whitebark pine (*Pinus albicaulis*). Under the future climate scenario, FIREBGC clearly indicates that the resulting more productive forest landscapes will generate more frequent and severe fires than the same landscapes experienced historically, even with the increase in annual precipitation

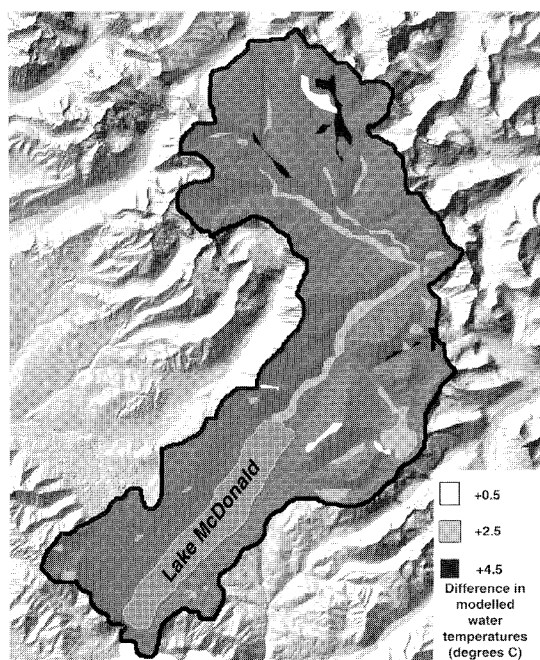


Figure 20.5 Relative change in modelled stream water temperatures from current climate to a future climate scenario. Note greater change in upper McDonald drainage relative to the rest of drainage area. Future climate scenario used a 30% increase in annual precipitation and + 0.5 °C warming

(Keane *et al.*, 1997). Keane *et al.* (1997) examined the interplay of different fire management policies, coupled with climate change, and asserted that fire-maintained early successional communities create overall landscapes that release less carbon to the atmosphere and are more diverse than landscapes without fire.

Scaling up to regional and global scales

The collection of modelling tools embodied in RHESSys and FIREBGC performed well for Glacier National Park and, in initial applications, expanded our understanding of mountain ecosystem responses to climate change and fire. Although designed as models that incorporate universal principles, much of the development was centred on the northern Rocky Mountains. It seemed important to apply these modelling

capabilities to other mountain ecosystems and regional landscapes to ensure that they performed equally well. We aimed to quantitatively examine how ecosystem processes differed within mountain protected areas and the larger, altered landscapes surrounding them. Regional scale forecasts of changes in ecosystem processes will suggest the future role of mountains in safeguarding biodiversity and providing ecosystem ‘services’ to society. These needs were addressed by establishing the mountain ecosystem transect from the Pacific Ocean to the Great Plains (Fagre and Peterson, 2000).

Regional scale

A simulation run for the entire region was completed using the model DAYMET (Thornton *et al.*, 1997). DAYMET builds on the logic and proven capabilities of MTCLIM (Running *et al.*, 1987) but extrapolates climate data three-dimensionally for entire landscapes (Thornton *et al.*, 1997), providing daily measures of temperature, precipitation, shortwave radiation and relative humidity. DAYMET maps deliver detailed, spatially-explicit estimates of daily climatology in remote and rugged mountainous areas that have no instrumentation and, hence, no local climate information. This allows us to compare patterns of alpine vegetation with climatic drivers over broad areas. For instance, the frost-free days that partially delimit the growing season for alpine plants can be mapped and compared to various plant community distributions. In the Bitterroot Mountains in Montana, we found that the variance in frost-free days is highest for the upper elevation sites that have the fewest frost-free days. Although these patterns have been documented for specific sites before, the DAYMET model’s capabilities make it possible to examine regional patterns for the first time.

Global scale

Trends in global mountain biodiversity should be contrasted with global-scale patterns in

vegetation cover and primary productivity. The dynamics of terrestrial landscapes are an integral part of global change processes and, for the first time, such large-scale dynamics are becoming available in near real-time. The TERRA satellite, launched in December 1999, has on board the MODerate resolution Imaging Spectroradiometer (MODIS), a sensor that can track the distribution, state and productivity of global vegetation each day at a 1-km² resolution (150 million pixel cells). These include cover type and vegetation density (LAI), net primary productivity and seasonality. This allows mountain ecologists to track seasonal trends in vegetation growth across entire mountain ranges by downloading weekly information from the Internet. Monitoring long-term changes in vegetation cover type by this means provides measures of landscape fragmentation within and around mountain environments, even in places where no field data exist. These perspectives will be a valuable adjunct to direct studies of mountain biodiversity at both regional and global scales.

Scaling down to specific communities in the landscape

In contrast to the regional scale picture of ecological dynamics across the mountain transect, our species-scale studies address interactions and biodiversity for specific components of the three mountain ecosystems. The examples below are integrated with the ecological modelling approaches previously described.

High-elevation forests

At all three parks, high-elevation tree species have responded where temperature and permanent snow coverage previously limited tree establishment and growth. In the Pacific north-west mountains, subalpine fir have been displacing subalpine meadows, particularly since the 1930s (Rocheftort and Peterson, 1996). This rapid regeneration of subalpine fir is most pronounced on the (wet) west side of the mountains during periods of warmer, drier climate and on

the (dry) east side of the mountains during periods of cooler, wetter climate. Precipitation is more critical than temperature where duration of snowpack limits length of the growing season (west side) and summer soil moisture limits seedling survival (east side). Analysis of repeat photographs in Glacier National Park has documented similar invasions of meadows by sub-alpine fir. If climate becomes warmer and drier during the next century, continued regeneration of trees may continue to displace meadows within wetter regions of the subalpine forest-meadow mosaic. More vigorous establishment and growth of high-elevation forests is also evident at the treeline. At Logan Pass in Glacier National Park, krummholz patches have expanded to fill inter-patch spaces, and krummholz have shifted to upright tree forms (Klasner and Fagre, in press). Although treelines generally have not moved upslope, the treeline ecotone throughout the park has become more abrupt as the density of krummholz increased (Butler *et al.*, 1994).

High-elevation forests at several locations in western North America have experienced increased growth rates, controlled by snowpack duration but presumably also related to increased atmospheric CO₂ or other factors (Peterson, 1998; McKenzie *et al.*, 2001). The response of tree growth to climatic variability is spatially and temporally variable with aspect, elevation, landform, soil and other site characteristics being important. Finally, a chronology of treeline expansion into alpine tundra has been documented in a few locations at Glacier National Park (Bekker *et al.*, 2000). Post Little Ice Age (ca. 1850) advances of sub-alpine fir krummholz occurred until the early 1900s in fingers extending into the alpine tundra, less than 100 m from the forest. However, numerous isolated trees and fingers of trees less than 80 years old have established as upright tree forms and up to several hundred metres from the forest. This indicates that limitations to seedling establishment and subsequent tree growth had been ameliorated, beginning about 1920. This corresponds to the rapid rise in summer average temperature that

is also related to the period of most rapid glacial recession (Fagre and Peterson, 2000).

Meadows

Biodiversity shifts in subalpine meadows and a high-elevation wetland in Glacier National Park have been studied by Lesica and Steele (1996) because they support the most diverse plant assemblages in the park and include numerous species at the edges of their ranges. These areas will act as climate change indicators because slight changes in moisture will eliminate marginal species. After only ten years, Lesica (2000) found four plant species declining but the trend was not statistically significant.

Non-native plants

At all three parks numerous non-native plants have established populations and are considered a management problem. At Olympic, there are nearly 1400 vascular plant species of which about 12% are non-native. At Glacier, there are 1150 vascular plants of which 10.5% are non-native. A distinct elevation gradient exists with most occurrences of non-native plants remaining at low elevations and relatively few in alpine areas. The extreme variability scenario (White *et al.*, 1998) indicates rapid transitions to grasses in lowland areas of the park where most roads, camp grounds, and buildings exist. This suggests a greater vulnerability to establishment of non-native species.

CONCLUSIONS

The multi-scale, multidisciplinary research and monitoring programme described here is a

nested approach that provides scientific insights for ecologists, park managers, and policy makers. It provides spatial and temporal continuity by using plot-level data as inputs to ecosystem simulation in broader landscapes and under possible future climates. It provides a bridge between fine-grained data at small spatial scales and coarse-grained data at sub-continental scales. Regional ecosystem models can play an important role in synthesising disparate existing information into an integrated assessment of the state of mountains and of the biodiversity they support.

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